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Retinal Projections in the Himé Salmon (Landlocked Red Salmon, *Oncorhynchus nerka*)

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ABSTRACT—The retinofugal projections in the himé salmon (landlocked red salmon, *Oncorhynchus nerka*) were studied by means of the Fink-Heimer method, and the anterograde horseradish peroxidase and cobaltic-lysine methods. The major projections were found on the contralateral side in the nucleus anterioris periventricularis of the preoptic area, the nucleus opticus dorsomedialis, the nucleus commissuralis posterioris, the nucleus geniculatus lateralis, the nucleus opticus accessorius, the area pretectalis and the optic tectum. Direct retinal projections were not found within the nuclear boundaries of the area ventralis telencephali pars supracommissuralis and the nucleus preopticus periventricularis which are known to play important roles in sexual behavior.

INTRODUCTION

In the himé salmon (landlocked red salmon, *Oncorhynchus nerka*), Takeuchi *et al.* [1] have shown that the key stimulus for the male courtship behavior is visual. Newcomb *et al.* [2] have reached a similar conclusion in the rainbow trout. On the other hand, localized brain lesion and stimulation experiments have shown that several restricted regions within the telencephalic and preoptic areas including the area ventralis telencephali pars supracommissuralis and the neighboring posterior ventral telencephalon (Vs-pVv), and the nucleus preopticus periventricularis (NPP) of the medial preoptic area (MPOA) are involved in the sexual behavior of himé salmon [3–6] and other fish species [7–13]. To understand the visual information processing in the brain during the sexual behavior, it is indispensable, in the first place, to know the retinal projection areas and then the relationship between these areas and the brain regions mentioned above which are supposed to be involved in the various aspects of the sexual behavior. In the present study, we examined the retinal projection areas of the himé salmon by means of Fink-Heimer method, and the anterograde HRP and cobaltic-lysine methods.

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MATERIALS AND METHODS

Fish

We used 41 male and female himé salmon (landlocked red salmon, *Oncorhynchus nerka*). Twenty-one fish were 25.0–31.5 cm in body length and were captured at the mouth of a river flowing into Lake Chuzenji (Nikko City, Japan) in September and October, during a homeward migration about 3 years after hatching. Twenty fish were 20.0–34.0 cm in body length and were obtained from May to August in a pond of National Research Institute of Aquaculture, Nikko branch, where they had been cultured for about 3 years.

Fink-Heimer method

Nine fish were used. The fish were anesthetized by immersing them in a 0.03% tricaine methanesulfonate (MS 222) solution. The right eye was enucleated unilaterally and the orbit was

filled with vaseline and dental resin. The fish were allowed to survive for 12–32 days at 9°C.

After the survival period, the fish were anesthetized with 0.03% MS 222 and perfused through the conus arteriosus with 0.7% NaCl solution, followed by 10% formalin-saline. The brains were removed from the skull and were postfixed in 10% formalin containing 10% sucrose for more than two weeks at 4°C. The brains were embedded in egg yolk, serial frontal sections were cut at 30 μm on a freezing microtome, and every fifth section was stained according to Ebbesson's modification of the Fink-Heimer method (Method 7 of [34]). The adjacent sections were stained with cresyl violet for histological identifications.

HRP method

Twenty-four fish were used. Eight to 20 μl of 20–25% HRP (Toyobo, Grade I-C) were applied in four ways as follows. First group (two fish) received unilateral intraocular HRP injection using a microsyringe. In the remaining three groups (22 fish), the conjunctival membrane surrounding the eye was excised and the extraocular muscles were severed. After cutting the optic nerve close to the eye ball, the eye ball was removed. In the second group (two fish), a glass capillary with a tapered tip filled with the HRP solution was pricked into the proximal end of the cut optic nerve and the capillary was secured using vaseline and dental resin. In the third group (17 fish), the cut optic nerve was drawn into a polyethylene tube. Vaseline was used to secure the tube to the orbit, and the tube was filled with the HRP solution using a microsyringe. After filling the tube, the open end of the tube was sealed with vaseline and the orbit was covered with the dental resin. In the fourth group (three fish), a piece of Gelfoam (Japan Upjohn Ltd.) soaked in the HRP solution was placed on the cut end of the optic nerve and the orbit was filled with vaseline.

The fish were postoperatively maintained at 9°C. One to 14 days after the HRP-injection, they were reanesthetized with MS 222 and were perfused through the conus arteriosus with 0.7% NaCl solution containing 5 IU/ml heparin, followed by the primary fixative containing 1% paraformaldehyde and 1.25% glutaraldehyde in 0.1 M phosphate buffer (pH 7.4) and then the secondary fixative containing 2.5% glutaraldehyde and 10% sucrose in 0.1 M phosphate buffer (pH 7.4). Immediately afterwards, the brains were dissected out and immersed in a 0.1 M phosphate buffer containing 30% sucrose for 12–24 hr. Serial frontal sections were cut at 40–60 μm on a freezing microtome and mounted on gelatinized slides. The sections were processed using Mesulam's tetramethylbenzidine method [35] and were counterstained with neutral red.

Caobaltic-lysine method

Eight fish were used. Under the MS 222 anesthesia, 10–20 μl of cobaltic lysine complex, prepared according to Görcs *et al.* [36], was applied unilaterally using the polyethylene tube in the same way as mentioned in the HRP method.

After the survival period between 7 and 14 days (at 9°C), the fish was decapitated. After dissecting out the brain, it was immersed in the 100 mM dibasic sodium phosphate solution saturated with H_2S for 20–30 min, fixed in 70% ethanol overnight, dehydrated, and embeded in paraffin. Serial frontal sections were cut at 40–50 μm and mounted on gelatinized slide. The CoS precipitate was intensified using the sodium tungstate developer according to Görcs *et al.* [36], and the sections were counterstained with neutral red.

Nomenclature

The terminology of the brain areas and nuclei was mainly after Northcutt and Davis [37] for the telencephalon, and Billard and Peter [38] and Nieuwenhuys and Pouwels [39] for the diencephalon and the mesencephalon (except optic tectum). We used the terminology of Vanegas *et al.* [40] for the optic tectum.

ABBREVIATIONS

AP	area pretectalis
C	cerebellum
Dc	area dorsalis telencephali pars centralis
Dd	area dorsalis telencephali pars dorsalis
Dld	area dorsalis telencephali pars lateralis dorsalis
Dlv	area dorsalis telencephali pars lateralis ventralis
Dm	area dorsalis telencephali pars medialis
Dp	area dorsalis telencephali pars posterioris
FDM	fasciculus dorsomedialis tractus optici

FR	fasciculus retroflexus
H	habenula
HOC	horizontal commissure
LI	lobus inferioris
LL	lemniscus lateralis
LPOA	lateral preoptic area
LV	nucleus lateralis valvulae
mOT	main optic tract
NAPv	nucleus anterioris periventricularis
NAT	nucleus anterior tuberis
NC	nucleus corticalis
NCP	nucleus commissuralis posterioris
NDL	nucleus dorsolateralis thalami
NDLI	nucleus diffusus lobi inferioris
NDM	nucleus dorsomedialis thalami
NDTL	nucleus diffusus tori lateralis
NE	nucleus entopeduncularis
NG	nucleus glomerulosus
NGL	nucleus geniculatus lateralis
NLTm	nucleus lateralis tuberis pars medialis
NNO	nucleus nervi oculomotorii
NOA	nucleus opticus accessorius
NODM	nucleus opticus dorsomedialis
NP	nucleus pretectalis
NPG	nucleus preglomerulosus
NPO	nucleus preopticus
NPP	nucleus preopticus periventricularis
NPPv	nucleus posterioris periventricularis
NPT	nucleus posterior tuberis
NR	nucleus rotundus
NRL	nucleus recessus lateralis
NVM	nucleus ventromedialis thalami
NSV	nucleus saccus vasculosus
OB	olfactory bulb
OC	optic chiasm
ON	optic nerve
OT	optic tract
PC	posterior commissure
SAC	stratum album centrale
SFGS	stratum fibrosum et griseum superficiale
SGC	stratum griseum centrale
SM	stratum marginale
SO	stratum opticum
SPV	stratum periventriculare
SV	saccus vasculosus
TEL	telencephalon
TeO	optic tectum
TL	torus longitudinalis
TMC	tractus mesencephalocerebellaris anterior
TOA	tractus opticus accessorius
TOI	tractus opticus intermedius
TOL	tractus opticus lateralis
TOM	tractus opticus medialis
TS	torus semicircularis
Vp	area telencephali pars postcommissuralis

RESULTS

The retinal projections were examined in the present experiments using three different methods: the Fink-Heimer, HRP, and cobalticlysine methods. Although the results obtained usings these methods were essentially similar, the cobalt-filling method was most sensitive and revealed the most extensive retinal projections. Therefore, the following description is mainly based on the results obtained using the cobalt-filling method.

In the present study, cobalt-filled fibers of passage were characterized by a smooth, elongated appearance. Terminal areas were characterized by randomly oriented thin varicose fibers intermingled with granular profiles. The former probably represent terminal axonal arborizations in the plane of sectioning and the latter probably those oriented perpendicular to it. Although the final decision as to whether these profiles really represent synaptic terminals awaits examinations at the electron microscopic level, the present definition of the fibers of passage and terminals seems to be apropriate [see 19, 21, 27–33].

The retinal projections of the himé salmon were mostly contralateral, but sparse ipsilateral projections were also seen. Extensive contralateral projections in the diencephalon and mesencephalon were grouped into seven major terminal areas: NAPv of the POA, nucleus opticus dorsomedialis (NODM) of Ebbesson [41], nucleus geniculatus lateralis (NGL), nucleus commissuralis posterioris (NCP), and nucleus opticus accessorius (NOA) of the diencephalon, and area pretectalis (AP) and optic tectum (TeO) of the mesencephalon.

Contralateral projections

Optic nerves, consisting of thick fibers, decussated at the optic chiasm (OC), and formed contralateral main optic tract (mOT) (Figs. 1A-D, 2). The main optic tract ran dorsocaudally toward the optic tectum, and at the level just rostral to the habenula, divided into three tracts; tractus opticus medialis (TOM), tractus opticus intermedius (TOI), and tractus opticus lateralis (TOL) (Figs. 1E, 3).

(1) POA and dorsal part of telencephalon

At the level of the rostral pole of the NAPv,

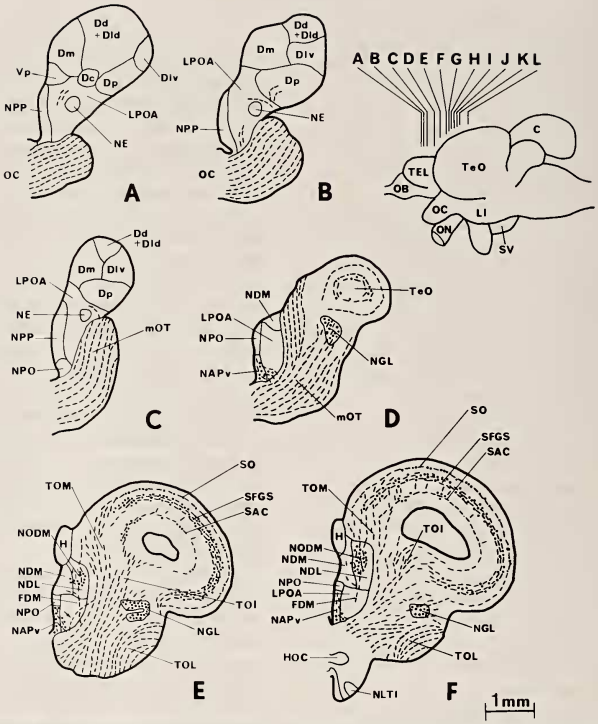

FIG. 1. Line drawings of frontal sections illustrating the retinal projections as determined using the cobaltic-lysine method. Dashes indicate cobalt-filled axons, while dots indicate cobalt-filled terminal fields. The inset shows the lateral view of the brain, and the levels of the sections are indicated.

several fine fibers branched from the main OT, ran dorsomedially in the ventral part of the LPOA, and terminated in the most rostral part of the NAPv (Figs. 1D, 4). Some of these fibers also terminated in the LPOA on the way to the NAPv. In some teleosts, this rostroventral part of the NAPv has been specifically named "the suprachiasmatic nucleus" [14, 19, 27]. After entering the NAPv, the fibers ran dorsocaudally along the ventricle and terminated in almost all parts of the NAPv (Fig. 1D-G). In the NPP and the NPO, neither retinal fibers nor terminals were seen (Fig. 1A-G).

A few fine fibers were seen in the posterodorsal telencephalon (Dp) (Fig. 1B) and the lateral preoptic area near the nucleus entopeduncularis and lateral to the NPP (Fig. 1A-C).

(2) Other diencephalic and mesencephalic areas

A) Nucleus geniculatus lateralis (NGL)

At the level of the habenula (H), the main OT entered the most rostral part of the NGL (Fig. 1D). The retinal terminals were seen in almost

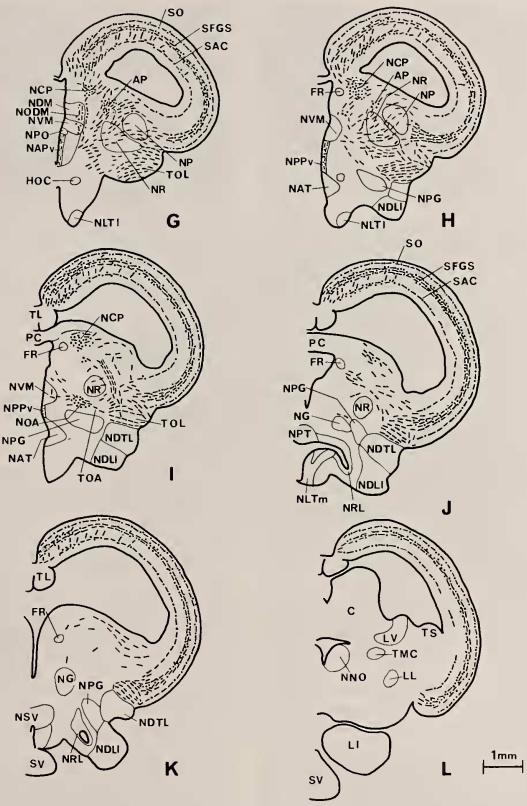

FIG. 1. Continued

entire part of the NGL, although the dorsolateral edge received heavier projections. In transverse sections both the NGL and the retinal terminal field appeared semilunar rostrally (Figs. 1D, 5A, B), U-shaped at the middle level with its opening facing medially (Figs. 1E, 3, 5C, D), and rectangular at the caudal level (Figs. 1F, 5E, F). Caudally, some fibers of the TOI passed through the NGL to enter the TeO. Recently, Braford and Northcutt [14] renamed the NGL as the superficial pretectal parvicellular nucleus, because of its topography and the lack of projection to the telencephalon like the mammalian NGL.

B) Nucleus opticus dorsomedialis (NODM)

At more caudal level than the anterior margin of the NGL, a diffuse fiber bundle (fasciculus dorsomedialis tractus optici, FDM) branched from the medial margin of the TOM, ran dorsally through

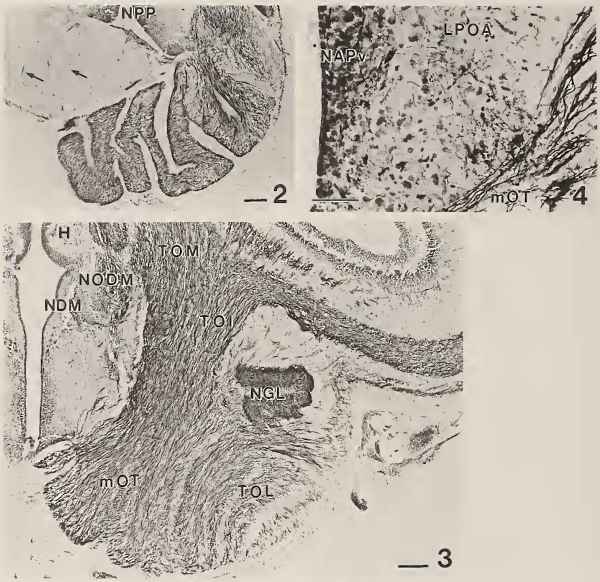

Fig. 2. Frontal section of the cobalt-filled optic nerve contralateral to the injection, at the level corresponding to that of Fig. 1A. A few cobalt-filled axons (arrows) also entered the ipsilateral optic nerve. Bar: 50 μm.

Fig. 3. Frontal section through the rostral part of the habenula (H). The main optic tract (mOT) branched into the tractus opticus medialis (TOM), tractus otpicus intermedius (TOI), and tractus opticus lateralis (TOL). Bar: 200 μm.

Fig. 4. Frontal section through the rostral part of the nucleus anterioris periventricularis (NAPv), at the level corresponding to that of Fig. 1D. Some cobalt-filled axons branched from the main optic tract (mOT) to enter the NAPv through the lateral preptic area (LPOA). 50 μm.

the LPOA, to reach the nucleus dorsolateralis thalami (NDL), and made a major termination area there (Figs. 1E, 3, 6A, B). In addition, a small branch of the FDM also terminated in the lateral part of the nucleus dorsomedialis thalami (NDM) (Fig. 1E-G). At about the same level as the FDM branched from the TOM, thick fibers branched from the TOM, ran dorsolaterally in the LPOA just lateral to the NAPv, and rejoined the TOM (arrow in Fig. 1E). Some of these fibers branched dorsally to contribute to the FDM. Some terminals were also seen in the nucleus ventromedialis thalami (NVM) which appeared ventral to the NDM at the caudal level of the habenula (Fig. 1G). These terminal areas ranging from the NDL to the lateral part of the NDM and the NVM seem to correspond collectively to the nucleus opticus dorsomedialis (NODM) of Ebbesson [41]. In the illustrations (Figs. 1, 3 and 6), the term "NODM" has been used in addition to "NDL", "NDM" and "NVM", to facilitate comparisons between Ebbesson's results [41] and ours. However, we should notice that the both nomenclatures are based on different criteria; the NODM of Ebbesson is a rather functional name, while the NDL, NDM and NVM are purely histological

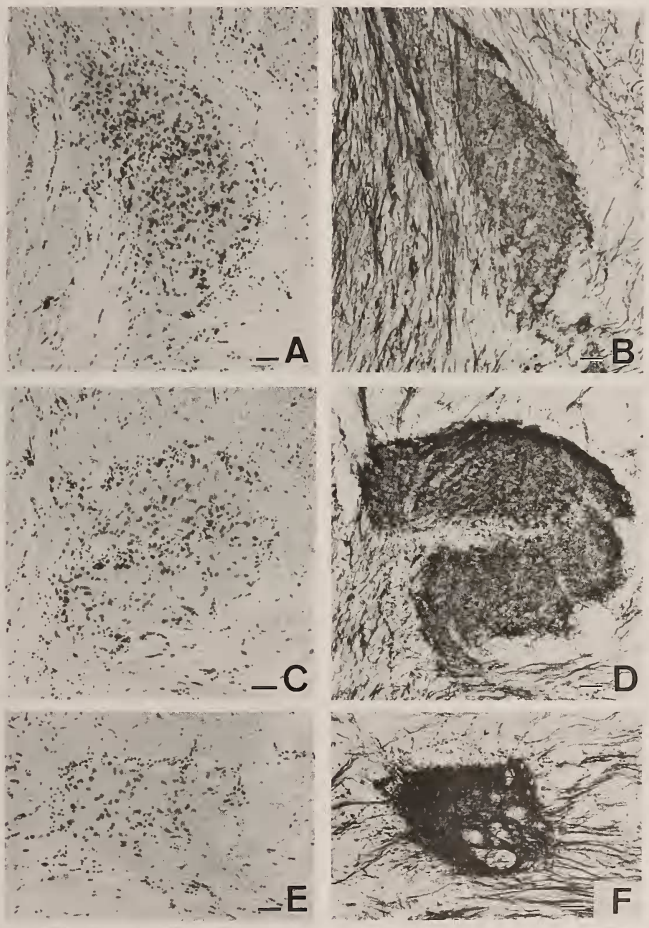

FIG. 5. Frontal sections of the Nissl-stained (A, C, E) and cobalt-labeled (B, D, F) nucleus geniculatus lateralis. A, B: rostral level, C, D: middle level, E. F: caudal level. Bar: 50 μm.

ones. The NODM of the himé salmon continued caudally to the level just rostral to the posterior commissure (Figs. 1E-G, 7D). A small number of fibers in the FDM ran dorsally through the NODM to enter the TeO, nucleus commissuralis posterioris and dorsal tegmentum (Fig. 1E-G).

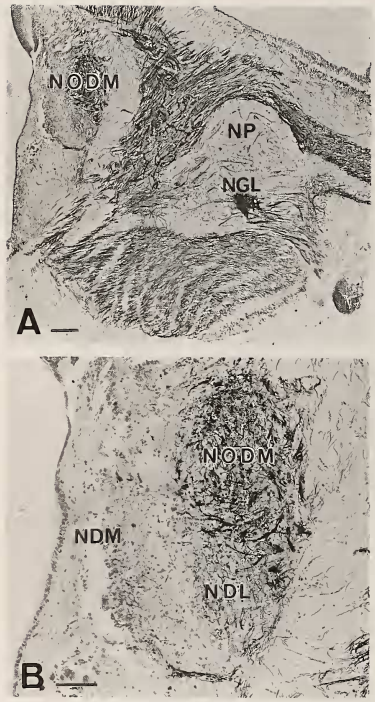

Fig. 6. A: Frontal section through the nucleus opticus dorsomedialis (NODM) and caudal part of the nucleus geniculatus lateralis (NGL). B: Higher magnification of the NODM shown in A. Cobalt-filled axon terminals of the NODM are distributed in the nucleus dorsolateralis thalami (NDL) and the lateral part of the nucleus dorsomedialis thalami (NDM). Bar: 200 μm (A) and 50 μm (B).

C) Nucleus commissuralis posterioris (NCP)

At the level caudal to the habenula, some fibers of the FDM ran through the NODM, entered the NCP, and terminated there (Figs. 1G-I, 7A, B). The NCP was located lateral to the fasciculus retroflexus (FR) and ventrolateral to the fibers of the posterior commissure, and was composed of sparsely distributed cells.

D) Nucleus posterioris periventricularis (NPPv)

At the level caudal to the horizontal commissure, the NAPv was gradually replaced caudally by the NPPv, which was situated dorsal to the nucleus anterior tuberis (NAT) and ventral to the NVM. Some retinal fibers entered the NPPv after running through the NAPv, and terminated there (Figs. 1H, I, 7A, C).

E) Area pretectalis (AP)

At the level where the NGL disappeared and the NCP appeared, the TOI entered the AP (Figs. 1G, 7D). Although the majority of the TOI fibers passed through the AP to the tegmentum and the TeO, some of them formed patch-like terminal fields within the AP (Figs. 1G, H, 7E). In Nissl-stained preparations, the AP was composed of sparsely distributed cells and the nuclear boundary was obscure. The AP was delineated medially by the NODM, dorsomedially by the NCP, ventrally by the nucleus rotundus (NR) which was a globular nucleus of closely packed small cells, and ventrolaterally by the nucleus pretectalis (NP) which consisted of rather sparsely distributed large cells. Several discrete fiber bundles ran through the NR and the NP on their way to the TeO and the TOL, without terminating there (Figs. 1G-I, 7F). At the caudal part of the AP, a thick bundle connecting the AP and the TOL was seen dorsolateral to the NR (Fig. 1I, arrow in Fig.7A).

F) Nucleus opticus accessorius (NOA)

A densely-packed fiber bundle (tractus opticus accessorius, TOA or basal optic tract) branched medially from the TOL and terminated in the area ventromedial to the NR and dorsal to the NPG (Figs. 1I, 7A). This area seems to correspond to the accessory or basal optic nucleus [15], although cells were scattered and the boundary was obscure in Nissl-stained preparations.

G) Optic tectum (TeO)

In the TeO, retinal fibers constituted three-layered terminal fields in the stratum opticum (SO), stratum fibrosum et griseum superficiale (SFGS) and stratum album centrale (SAC) (Figs. 1E-L, 8A). Small number of fibers in the SAC sometimes invaded the stratum periventriculare (SPV). Some fibers ran through the stratum griseum centrale (SGC) between the SAC and the SFGS (Fig. 8A-C). In the SO and SFGS, many

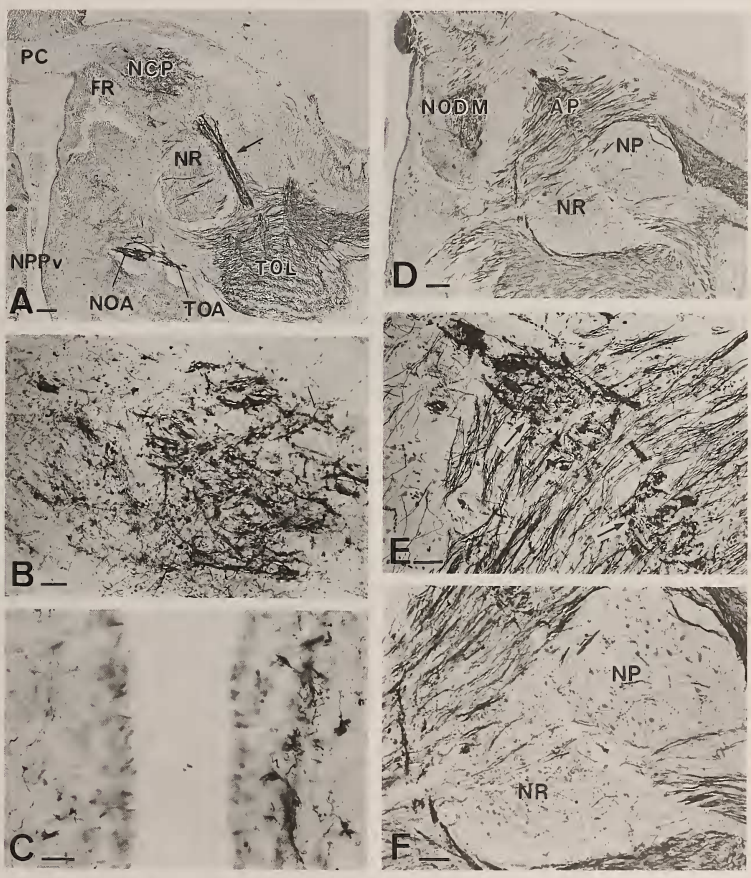

FIG. 7. A: Frontal section through the nucleus commissuralis posterioris (NCP), nucleus posterioris periventricularis (NPPv) and the nucleus opticus accessorius (NOA). A thick fiber bundle (arrow) connects the rostrally distributed area protectalis (Fig. 7D) and the tractus opticus lateralis (TOL). B: Higher magnification of the terminal area in the NCP shown in A. C: Higher magnification of the axon terminals in the NPPv shown in A. D: Frontal section through the area pretectalis (AP) and the nucleus opticus dorsomedialis (NODM), at the level corresponding to that of Fig. 1G. E: Higher magnificantion of the AP shown in D. Cobalt-filled fibers formed patch-like terminal fields (arrows). F: Higher magnification of the nucleus rotundus (NR) and the nucleus pretectalis (NP) shown in D. Some cobalt-filled fibers passed through the NR and the NP. Bar: 200 μm (A, D), 50 μm (B, E) 20 μm (C) and 100 μm (F).

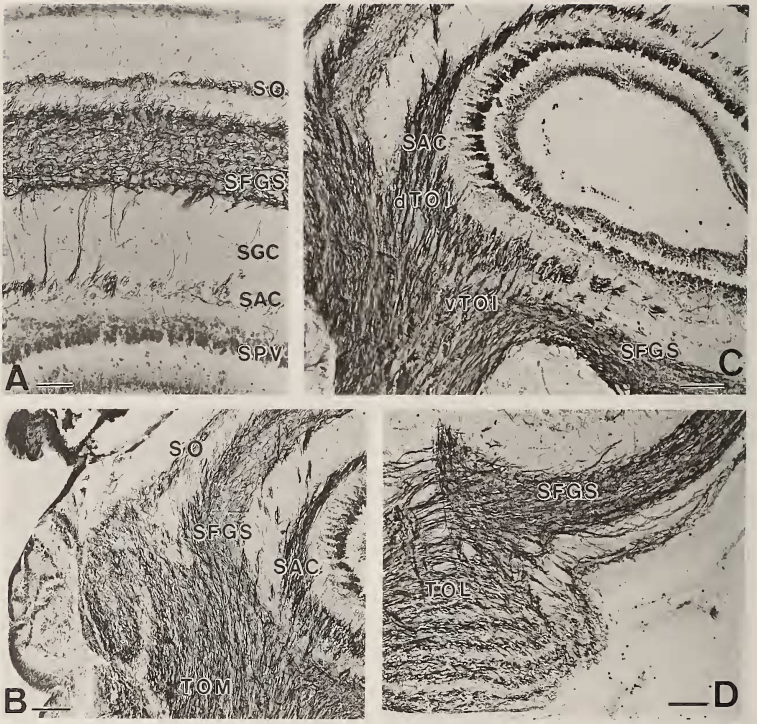

Fig. 8. Frontal sections showing the cobalt-filled axons and terminals in the optic tectum. A: Three-layered terminal fields in the stratum opticum (SO), stratum fibrosum et griseum superficiale (SFGS) and the stratum album centrale (SAC). B: The tractus opticus medialis (TOM) entered mainly the SO and the SFGS. C: The tractus opticus intermedius (TOI) branched into the dorsomedial (dTOI) and ventrolateral (vTOI) divisions. The dTOI mainly entered the SAC, while the vTOI mainly entered the SO and SFGS. D: The tractus opticus lateralis (TOL) entered mainly the SO and SFGS. Scale bar: 100 μm (A), 20 μm (B, C, D).

terminals were seen throughout the TeO. In the SAC, fibers and terminals were also distributed throughout the TeO, although more terminals were seen in the dorsomedial portion.

Fibers of the all three tracts (TOM, TOI, and TOL) contributed to these projections, although the course and the major stratum of termination were different among these tracts. The TOM entered the rostromedial portion of the TeO. Majority of fibers in the TOM projected to the SO and SFGS, and some entered the SAC (Fig. 8B). The TOI was divided into the dorsomedial (dTOI) and ventrolateral (vTOI) branches at the entrance to the ventral portion of the TeO (Fig. 8C). The dorsomedial branch mainly entered the deep layer (SAC), while the ventrolateral branch ran through the tegmentum and mainly entered the intermediate layer (SFGS), and also made a minor projec-

tion to the deep layer (SAC). More caudally than the TOM and the TOI, the TOL entered the ventrolateral portion of the TeO. It terminated mainly in the SO and SFGS (Fig. 8D).

Ipsilateral projections

Ipsilateral retinal projections were observed in the NAPv, NODM, AP, NCP, and NOA, but not in the NGL and TeO, although they were fewer and sparser compared with the contralateral projections.

A few fibers were seen in the ipsilateral optic nerve at the optic chiasm (arrows in Fig. 2), which indicates the presence of retinal fibers running directly into the ipsilateral brain without decussating.

In the gray matter connecting both sides of the NAPv which made up the floor of the third ventricle, several recrossing fibers were seen running from the contralateral NAPv into the ipsilateral NAPv (arrowhead in Fig. 9). These recrossing fibers were seen rostrally from the level of the optic chiasm, and caudally to that of the horizontal commissure.

In the horizontal commisure, the posterior commissure, and the intertectal commissure, however, such recrossing fibers were never seen.

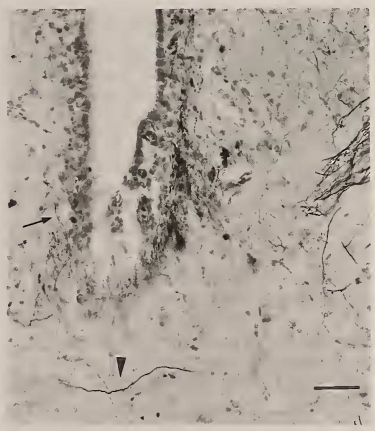

Fig. 9. Frontal section through the nucleus anterioris periventricularis (NAPv). Several cobalt-filled axons (arrowhead) recrossed to enter the NAPv (arrow) ipsilateral to the injected optic nerve. Scale bar: 50 μm.

Projection areas revealed by the Fink-Heimer and HRP methods

(1) Fink-Heimer method

In the POA, anterogradely degenerating fibers and terminals were observed in the LPOA lateral to the NAPv, but none of these degenerating fibers entered the NAPv. Similarly, degenerations were not observed in the LPOA lateral to the NPP where several cobalt-labeled fibers were seen.

Among the six major terminal areas in the diencephalon and midbrain reveraled by the cobalt-filling method, many degenerating terminals were observed in the NODM, NCP, NGL, AP, and TeO, but only a few degenerating terminals were seen in the NOA.

A few silver grains were seen in the ipsilateral LPOA and NODM, indicating the presence of terminals. Since they were very sparsely distributed, it was often difficult to discriminate them from the background.

(2) HRP method

Among the four HRP-application methods, the method using the polyethylene tube revealed the most extensive retinal projections. In these materials, many HRP-labeled fibers were seen in all the major terminal areas shown by the cobalt-filling method. However, ipsilateral projections were never observed.

DISCUSSION

In the present study, the cobaltic-lysine method proved to be the most sensitive one, since the most extensive retinal projections were demonstrated by this method in comparison with the Fink-Heimer and HRP methods. Other similar cobalt-filling methods such as those using cobaltous-lysine [31–33] and cobalt chloride [30] have shown more extensive retinal projections than autoradiographic or anterograde degeneration methods in the goldfish, cichlid fish, and eel. Since it is not probable that the cobalt complex is transported transneuronally [31], the retinal projections shown in the present study can be regarded as truly primary projections.

In the himé salmon (the present study), the

NAPv received direct bilateral retinal projections, although the ipsilateral projections were scarce. In the LPOA lateral to the NPP, several retinal fibers of passage, not terminals, were recognized. In the NPP and the NPO, neither the retinal fibers nor the terminals were seen.

The direct retinal projection to the MPOA has so far been reported in many teleost species, but somewhat different results have been obtained depending on the species and the experimental methods.

It has been shown in some teleosts that the nucleus opticus hypothalami (NOH), which seems to correspond to the NAPv, or a part of the NAPv of the present study from the cytoarchitectural similarity, receive bilateral [14, 19, 23, 30], or contralateral [16, 22] retinal projections. It has also been reported that the region which might correspond to the NAPv of the present study receives bilateral [17, 21, 26] and contralateral [18, 25] retinal projections. The present study showed that there was no direct retinal projections to the NPO. It has, however, been shown in several teleosts that the nucleus opticus hypothalamicus, pars magnocellularis (NOHpm) or the nucleus preopticus pars magnocellularis (NPM), which seems to correspond to the NPO of the present study from the cytoarchitectural similarity, receives bilateral [23] or contralateral [16, 24] retinal projections.

Presence of direct retinal projections in the NPP seems to be still controversial. Reperant and Lemire [23] have reported in cyprinids the direct retinal projections in the "vicinity of the contralateral wall of the third ventricle" rostral to the NOHpm, which possibly corresponds to the NPP of the present study. In the goldfish, Springer and Gaffney [31] have found, using the cobaltous-lysine method, that the retinal projections to the POA are "far more complex than previously considered", and have reported four major fiber distributions (H1-H4) within the POA. It is inferred from their illustrations that the NPO and the NAPv, but not the NPP receive the direct bilateral retinal projections in the goldfish.

The retinal projections have been examined in many teleost species using the anterograde degeneration methods [14–26], autoradiographic method [14, 17, 21–23, 26, 27], horseradish peroxidase (HRP) method [19, 21, 27–29] and cobalt-filling method [30–33]. In spite of some minor differences, there seems to be a general agreement that the optic tectum (TeO) receives a major retinal projection, and several diencephalic and mesencephalic areas receive some minor retinal projections. Although the cytoarchitecture of the telencephalon and the preoptic area is basically similar among teleosts, there are some interspecific variations in that of the diencephalon and the mesencephalon. In addition, the ambiguity of the cytoarchitectural description and the lack of uniformity of nomenclature have made it very difficult to compare retinal projections in the diencephalon and the mesencephalon among different teleost species. Therefore, we focus on the comparison of the retinal projections in areas other than the MPOA between *Salmo* and *Oncorhynchus*.

The retinal projections of the rainbow trout (*Salmo gairdneri*) have been studied using the Fink-Heimer and the autoradiographic methods [22]. The comparison of retinal projections between the rainbow trout and the himé salmon in the present study revealed the following similarities and differences. In both the rainbow trout and the himé salmon, the optic tract is divided into three bundles. Furthermore, the centrum opticum thalamicum (corresponding to the NODM of the present study), centrum opticum thalamo-pretectale (corresponding to the NCP of the present study), centrum opticum basale thalami (corresponding to the NOA of the present study), centrum opticum pretectale (corresponding to the AP of the present study), and TeO receive contralateral retinal projections.

On the contrary, there are several differences in the retinal projections between the two: (a) A few retinal fibers were seen in the Dp of the himé salmon, while no such fibers were described in the rainbow trout. (b) Sparse ipsilateral projections to the NODM, the NCP, and the AP were seen in the himé salmon, while the retinal projections of the rainbow trout were completely contralateral. (c) In the himé salmon, the retinal fibers in the SO, SFGS and SAC were seen throughout the TeO. In the rainbow trout, however, the retinal fibers in the SAC were restricted in the dorsomedial part of

the TeO, although those in the SO and SFGS were seen throughout the TeO. (d) In the rainbow trout, the centrum opticum laterale thalami, medial to the area thalamica lateralis which seems to correspond to the nucleus rotundus of the present study, receives contralateral retinal projections.

It is a future problem to know how the visual informations conveyed from the retina to the projection areas clarified in the present study reach the brain regions involved in the sexual behavior (Vs-pVv, NPP, etc.).

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